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Energy metabolism in women during short exposure to the thermoneutral zone

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Abstract

Ambient temperature has been shown to affect energy metabolism in field situations. Therefore, we assessed the effect of a short exposure to the thermoneutral zone, i.e., 27 °C (81 °F), in comparison to the usual ambient temperature of 22 °C (72 °F), on energy expenditure (EE), substrate oxidation, and energy intake (EI) in a controlled situation. Subjects, i.e., women (ages 22 ± 2 years, BMI 22 ± 3, 28 ± 4% body fat), stayed in a respiration chamber three times for 48 h each: once at 22 °C, and twice at 27 °C in random order, wearing standardized clothing, executing a standardized daily-activities protocol, and being fed in energy balance (EB). During the last 24 h at 22 °C, and once during the last 24 h at 27 °C, they were fed ad libitum. At 27 °C, compared to at 22 °C, EE was 8.9 ± 1.3 MJ/day vs. 9.9 ± 1.5 MJ/day ($P < .001$) due to decreases in diet-induced thermogenesis (DIT) and activity-induced energy expenditure (AEE) ($P < .01$); respiratory quotient (RQ) had increased ($P < .05$); core ($P < .05$) and skin ($P < .001$) temperatures had increased. During ad lib feeding, EI was 90–91% of EE ($P = .9$), due to changes in energy density (ED) of the food choice ($P < .01$), and related to changes in body temperature and EE ($P < .001$). Thus, at 27 °C, compared to 22 °C, energy metabolism was reduced by reductions in DIT and in AEE, while RQ was increased. Reduction in EI was primarily related to body temperature changes and secondarily to changes in EE.

Keywords: Ambient temperature; Body temperature; Energy expenditure; Substrate oxidation; Energy intake; Energy density; Appetite; Humans

1. Introduction

Ambient temperature has been shown to affect energy metabolism in field situations. In this controlled study, we addressed the questions whether ambient temperature in the zone of thermoneutrality 27 °C (81 °F) affects energy metabolism under energy balance (EB) conditions, and energy intake (EI) under ad lib feeding conditions, as compared to the temperature the subjects were acclimated to, namely, 22 °C (72 °F). 22 °C is the normal temperature in the rooms and buildings in The Netherlands. Within a certain range of ambient temperatures, homeotherms, e.g., humans, have a relatively constant core body temperature [1–6] that represents the temperature of deep thermosensitive units and the thermal mass of the body core [7]. The skin temperature varies relatively more with the temperature of the environment and with metabolic rate than the core temperature does. It contributes to the control of skin blood flow in neutral and warm conditions thus influencing the effective thickness of the body 'shell' according to the core–shell concept [3,8,9]. A significant relationship between body temperature and average daily metabolic rate [4,10–12], as well as between ambient temperature and metabolic rate, has been shown. In older [13–17] and more recent studies [18–20], an inverse relationship between heat production or metabolic rate and ambient temperatures between 10 and 30 °C was shown. Changes in energy metabolism related to the actual ambient temperature in homeotherms, e.g., humans, were observed as changes in total or in basal metabolic rate (BMR). Effects on activity-induced energy expenditure (AEE) [21] and diet-induced thermogenesis (DIT) [22] only have been dealt with independently. The aim of the present study was to highlight EB in women exposed to the thermoneutral zone, in comparison to the usual temperature in the buildings, i.e., the temperature they were acclimated to, wearing 0.6 clo of insulation. EB was assessed in a behavioral–physiological way. The

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relationship between a physiological response (energy expenditure [EE] and core skin temperature gradient controlled for clothing and daily physical activities) and a behavioral response (the appetite profile and ad libitum food intake) to an elevated ambient temperature was assessed. The interesting part of this possible relationship is the question whether ad libitum food intake is primarily related to ambient temperature, thus to the core–skin temperature gradient of the body, or to EE. The present study addresses the effect of a short-term exposure to the thermoneutral zone 27 °C (81 °F) in a well-controlled but relatively normal situation on total EE and on the separate components of it at the same time, in EB conditions. To study AEE in the thermoneutral zone, it was necessary for the daily physical activities to follow a standardized protocol. Studying DIT in the thermoneutral zone also necessitates accounting for possible EI adaptation [23–26]. Furthermore, a possible effect on substrate oxidation was assessed. In addition to assessing the effect of a change in ambient temperature on EE, we measured the effect on EI under ad libitum conditions at the same time. With respect to the relationship between food intake and ambient temperature, increased ambient temperature is generally considered to inhibit appetite. Although LeBlanc [27] reports no change, Edholm and Goldsmith [28], in a study of physically active acclimatized and unacclimatized soldiers deployed to a cold environment, found food consumption increased with exposure to cold climate. Johnson and Kark [29] showed EI decreases with increasing average local temperature. While assessing the possible change in EI in humans in response to short-term exposure to an elevated ambient temperature, we took the possible changes in EE into account, by assessing the EE while the subjects were fed in EB separately, as mentioned above. At both temperatures, daily physical activities and clothing were the same for all subjects and at each occasion. We hypothesized that both expenditure and intake of energy would decrease in the zone of thermoneutrality, in comparison with energy metabolism below the zone of thermoneutrality, at the temperature the subjects were acclimated to.

2. Methods

2.1. Subjects

Eight healthy female volunteers participated in this study. They were recruited from the University staff and students. Physical characteristics [mean; S.E.M.: age (years) 22.6; 1.8, height (m) 1.69; 0.06, weight (kg) 63.9; 11.0, BMI (kg/m^2) 22.2; 3.2, body fat% 27.8; 4.4, fat-free mass (FFM) (kg) 48.1; 5.8] show that all subjects were normal in weight. Body composition was determined in the fasted state by hydrodensitometry with simultaneous assessment of the residual lung volume by a helium dilution technique. Percentage body fat was calculated using the equation of Siri [30]. Scores on the Three Factor Eating Questionnaire [31] [F1 (cognitive restraint): 7 ± 2; F2 (disinhibition or emotional eating): 5 ± 3; F3 (hunger): 5 ± 2] showed that the subjects were dietary unrestrained, with normal values for disinhibition or emotional eating and hunger, relative to our population [32]. Exclusion criteria were: medication, intensive sports activities (>4 times a week), smoking, unhealthy with respect to blood pressure, diabetes, other illnesses, being overweight or obese, dietary restraint. The subjects were asked which percentage of time they usually spend inside and outside buildings, and the temperature of the buildings they usually live and work in. Only one gender was chosen to limit the number of subjects. The subjects were informed on the nature of the experiment, especially on what to expect from staying in a respiration chamber. The chamber was shown to them before the experiment, and the principle of the measurements was explained to them. They were required to follow the detailed instructions on clothing, time schedule, daily activities, meals and snacks, rating of questionnaires as described below. All subjects signed an informed consent for the study protocol, which was approved by the Medical Ethics Committee of the University of Maastricht. The motivation for participation of the subjects was scientific interest; this was the first time such a study was performed in the respiration chambers at the University of Maastricht. As such, the subjects were not naïve in regard to the nature of the research, but we all were naïve in regard to the expected outcomes.

2.2. Protocol

The study took place at the Department of Human Biology, University of Maastricht. Subjects stayed three times for 48 h each (21:00–21:00 h) in the respiration chamber; once at the acclimation temperature, i.e., 22 °C (72 °F), and twice in the thermoneutral zone, i.e., 27 °C (81 °F); the three sessions were performed in random order, with 4 weeks in between the sessions. At 22 °C and once at 27 °C, subjects were fed in EB on the first day, and ad libitum on the second day. During the other 2 days at 27 °C, they were fed in EB. This experimental set-up allowed one habituation day, both times at 27 °C. The second days at 27 °C could then be used for comparisons: one for EE and one for EI. The acclimation temperature of 22 °C was based upon the usual environment the subjects. They were living in centrally heated houses (22–23 °C), and working in centrally heated buildings (22 °C). They reported spending 6–12% of their waking time during the working days of the week outside, by cycling to and from work, and shopping. At that time of the year, outside temperature was 10 ± 2 °C, and the insulation of outdoor clothing was 1.6 ± 0.2 clo [35]. Each time a subject stayed in the chamber, she was in the same phase of her menstrual cycle, to avoid possible effects of menstrual cycle phases on EE. Thus, a within-subject design was applied.

2.3. Respiration chamber

The respiration chambers consist of two adjoining 14 m^3 rooms, each furnished with a bed, chair, television, radio, telephone, intercom, computer, wash bowl, and deep freeze toilet. The chambers give the impression of a normal living room. For each experiment, two subjects are present at the same time, one in each room. Communication between the subjects and investigator is possible via an intercom or telephone. Visual contact is also possible through a window in the door and between the two chambers. A third window provides outside view. Three air locks provide passage for the exchange of food, collection of urine, and for sampling of blood. During the experiment, the temperature as well as the relative humidity (55% rh) was almost constant in the chamber, at 22 or 27 °C, during day and night. The measured temperature varied between 21.9–22.1 and 26.9–27.1 °C, respectively. The variation in relative humidity was 53–55% rh [33]. Physical activity was monitored by means of a radar system, based on the Doppler principle [33], validated by Bouten et al. [34].

2.4. Outfit

Subjects were required to wear the same outfit three times: underwear, bermuda shorts, two T-shirts, and a pair of sport shoes during the day (insulation 0.6 clo [35]). At night, subjects wore one T-shirt and they slept under a cotton sheet and a light duvet (375 g/m^2). The clothing was tried out before the protocol began to assure comfort at 27 °C as well as at 22 °C. The subjects received instructions on the clothing beforehand. It was explained to them that they had to wear the same outfit every time in order to allow us to compare exposure to two different ambient temperatures, without possible behavioral adaptation to ambient temperature by means of clothing.

2.5. Body weight measurement and daily-activities protocol

Body weight was determined on a digital scale, accurate to the nearest 0.1 kg, at the start and at the end of each session, at 21:00 h. Moreover, subjects were instructed to weigh themselves in the chamber, every morning in the fasting state, after voiding.

They were also instructed to follow a standard daily-activities protocol, which described every hour, and sometimes every 15 min, what the subjects were supposed to do. It included household activities, standardized extensive aerobic exercise, refreshing, and sedentary activities such as reading and watching television. The meal and snack times were standardized. The aerobic exercise was standardized by consistently using the same music with a fixed rhythm from a radio-cassette, while the subjects performed the same step test (alternating 5 min stepping, 5 min sitting), during 30 min, once in the morning and once in the afternoon, controlled by the experimenter.

2.6. Body temperature

Subjects' skin temperatures were registered continuously from 8:00 a.m. to 12:00 p.m. by means of a thermistor surface contact probe (YSI Series 400 probes; accuracy ±0.01 °C) fixed to the skin with thin, air-permeable adhesive surgical tape. Proximal skin temperatures were measured at the forehead, thigh, and the infraclaviculaire zone; distal skin temperatures were measured at the hand and foot. Core temperature was measured rectally, from 00:00 h till 8:00 a.m., by means of a similar thermistor probe (YSI Series 400, accuracy ±0.1 °C); insertion was 4 cm. During the day, rectal temperature was measured using a conventional digital thermometer (Philips HP 5315, accuracy 0.1 °C); insertion was 10 cm. Temperature measurements were thoroughly explained to the subjects, and they were trained in the preprotocol phase in order to obtain reproducible measurements, before entering the respiration chambers. The thermometric probes were calibrated to within 0.05 °C in a water bath against a reference mercury thermometer (accuracy ±0.02 °C).

2.7. Energy expenditure

Subjects' EE was calculated from oxygen consumption and carbon dioxide production [33,36]. The respiration chamber was ventilated with fresh air at a rate of 70–80 l/min. A dry gas meter (G4 Schlumberger, The Netherlands) measured the ventilation rate. A paramagnetic O_2 analyzer (OA 184A, Servomex) and an infrared CO_2 analyzer (Uras 3G, Hartmann and Braun) were used to analyze the samples of the in- and outgoing air. Ingoing air was analyzed once every 15 min and outgoing air every 5 min [33].

2.8. Energy intake

Subjects' appetite and EI were determined as follows. At 22 °C and once at 27 °C, subjects were fed in EB during the first 24 h, and ad libitum during the second 24 h. The other time the subjects stayed at 27 °C, they were fed in EB throughout the 48 h. Feeding in EB took place by estimating EE by means of the Harris–Benedict equation [37], which gives the BMR, and multiplying the BMR by an estimated physical activity level (PAL) of 1.65 [38]. After measuring EE, this estimation was adjusted to the realistic BMR and PAL. Thus, energy requirement was calculated for each subject individually. Based upon this, the meals and snacks were prepared (three meals and three snacks per day, which was on average the subjects' habitual food intake pattern), using comparable food items each day, which also belonged to the subjects' habitual diets. Breakfast consisted of whole wheat bread (10.5 kJ/g), apricot jam and blueberry jam (10.2 kJ/g), sweet spicy biscuit (20.5 kJ/g), coffee (decaffeinated), tea, or water (0 kJ/g). Snacks were choco-wafer cookies (20.2 kJ/g), wheat cookies (17.3 kJ/g), cake (17.6 kJ/g), and unsweetened orange juice (1.6 kJ/g), fruit

(apple 2.1 kJ/g, banana 3.8 kJ/g, kiwi 1.7 kJ/g, mandarin orange 2.0 kJ/g), paprika crisps and salt crisps (22.6 kJ/g). Lunch consisted of lasagna bolognaise, macaroni with cheese and ham or nasi goreng (all 5.4 kJ/g), water, vanilla ice cream (5.1 kJ/g), milk chocolate (22.5 kJ/g), water. Dinner consisted of toast or sandwich (15.3 kJ/g) with Gouda cheese 48+ (16.4 kJ/g), ham (5.7 kJ/g), salad 0.3 kJ/g, tomato (0.5 kJ/g), full fat fruit yogurt or vanilla dessert (3.9 kJ/g), and water.

All food items were checked for hedonic values beforehand, and only the ones that were liked by all subjects [Visual Analog Scale (VAS) recording at least 60 mm] were included in the menus. All these foods and drinks were of known composition and were weighed before and after each meal or snack occasion to the nearest 0.1 g. The energy content and composition of each diet was calculated using the Dutch food composition table [39].

Macronutrient composition (carbohydrate/protein/fat: 55/14/31 percentage of energy at 22 °C, and 57/14/29 percentage of energy at 27°) and energy density (ED, 2.9 kJ/g at 22 °C and 2.7 kJ/g at 27 °C) were kept at comparable values. The food items were the same at both ambient temperatures and only the amounts were adapted to the energy requirements. ED decreases when offering a lower EI, but still keeping the weight of the food the same. Because ED was not decreased only by water, there was a slight difference in the macronutrient composition.

When the subjects were fed ad lib, they could order any food from the list at any time by telephone. Appetite profiles, i.e., the subjective feelings of motivation to eat, were assessed before and after breakfast, midmorning, before and after lunch, in the afternoon, before and after dinner, and once in the evening, by ratings on 100-mm long anchored VASs [38], with the following questions: How hungry, full, satiated, thirsty are you (anchored: not at all, very)? How much do you estimate you could eat (anchored: nothing/very much)? How is your desire to eat? How is your appetite (anchored: very weak/very strong)? During feeding in EB, appetite was recorded only by VASs [38].

2.9. Comfort

Comfort ratings representing general physical wellbeing were monitored nine times in the course of each experimental day using 100 mm VAS. The questions asked how comfortable, satisfied, irritated, fit the subjects felt, how agreeable the ambient temperature was found, and whether the clothing was found to be adapted to the surrounding temperature (anchored: not at all; very).

2.10. Data analysis

To check whether the subjects were in EB, the difference in 24 h EE and EI was calculated for each situation (the EB as well as the ad lib situations at both ambient temperatures). Then, the differences between EE and EI were compared with a theoretical difference: 0, indicating no difference between EI and EE, thus a neutral EB.

We compared the periods of 24 h when the subjects were fed in EB: Day 2 at 27 °C vs. Day 1 at 22 °C. Separately, we compared the days when they were fed ad lib following a day in EB: Day 2 at 27 °C (ad lib) vs. Day 2 at 22 °C. The rationale for this was that at 22 °C, habituation with respect to ambient temperature was not necessary, so both days at 22 °C could be used. However, at 27 °C, the first day was considered as a day for habituation. Therefore, the second days at 27 °C was used for comparisons, once to compare EE, and once to compare ad lib food intake on a day after having been fed in EB.

Comparisons were made with respect to the following aspects:

- 24 h EE (EE in MJ/day) and respiratory quotient (RQ) [36].
- Sleeping metabolic rate (SMR): the lowest mean EE over three consecutive hours between 24:00 and 07:00 h [33,34,38]. Accuracy of an individual SMR measurement is given by its standard deviation of the seven measurement points during the three consecutive hours.
- 24 h DIT: the increase of EE above SMR, corrected for AEE. This was achieved by plotting EE against radar output, for each individual in each session. The intercept of the regression line, at the offset of the radar, thus at zero physical activity, represents the EE in the inactive state: resting energy expenditure (RMR), consisting of SMR and DIT. The accuracy of RMR is given by the 95% confidence interval of the individual regression lines.
- DIT was calculated by subtracting SMR from RMR [23–25,38].
- AEE: total EE − RMR [23–25,38] as a function of radar output, corrected for the offset point of the radar. The calculation of AEE based upon the radar output had been validated using a triaxial accelerometer, showing an r^2 of .9; $P < .0001$ [34]. The 95% confidence interval of the individual regressions of accelerometer counts and radar output was $2 \pm 1.4\%$ of AEE [34].
- PAL: 24 h EE/SMR.
- RQ: $V\mathrm{CO}_2/V\mathrm{O}_2$.
- Food quotient (FQ) as $V\mathrm{CO}_2/V\mathrm{O}_2$, when the food consumed is oxidized completely. O_2 consumption (l/day) = 0.966 × protein intake (g) + 2.019 × fat intake (g) + 0.829 × CHO intake (g). CO_2 production (l/day) = 0.774 × protein intake (g) + 1.427 × fat intake (g) + 0.829 × CHO intake (g) [40].
- The 16 h averages of the ratings on the components of the appetite profile and of the comfort ratings.
- Body temperatures (rectal and skin temperatures)

During the ad lib feeding days, total EI, EI as a percentage of EE, macronutrient composition of EI, ED [total EI divided by total weight of consumption (including water)] were calculated.

Comparisons were made using ANOVA repeated measures. A multiple regression analysis was executed on the

possible contributions of changes in body temperature and in EE to possible changes in EI. Statistical analyses were performed using the statistical software program STATVIEW SE + GRAPHICS (Abacus concepts, Berkeley, CA). Outcomes were regarded as statistically different if $P < .05$.

3. Results

As indicated before, the comparisons made for the 24 h EB periods concerned Day 2 at 27 °C (EB) vs. Day 1 at 22 °C; for the 24 h ad lib periods this concerned Day 2 at 27 °C (ad lib) vs. Day 2 at 22 °C.

3.1. Body weight

Body weight in the fasting state remained constant at 63.9 ± 11.0 kg over each experimental 48-h period. Moreover, it remained constant over the whole experimental period (63.8–64.0 ± 11.5 kg).

3.2. Body temperature

In EB, at 27 °C compared to 22 °C, core ($P < .05$), proximal and distal ($P < .001$) skin temperatures had increased (Fig. 1), while the differences between rectal and distal temperatures had decreased ($P < .01$).

3.3. Energy balance

During the 24 h under EB conditions EI minus EE was + 0.2 ± 0.7 MJ/day at 22 °C, and + 0.4 ± 0.3 MJ/day at 27 °C, which was neither statistically different from each other, nor statistically different from zero ($P > .5$), indicating that the subjects were in EB indeed. Moreover, calculated EI from estimated RMR from the Harris–Benedict equation and a PAL of 1.65 were hardly different from the calculation based upon the measured BMR and PAL from the previous day.

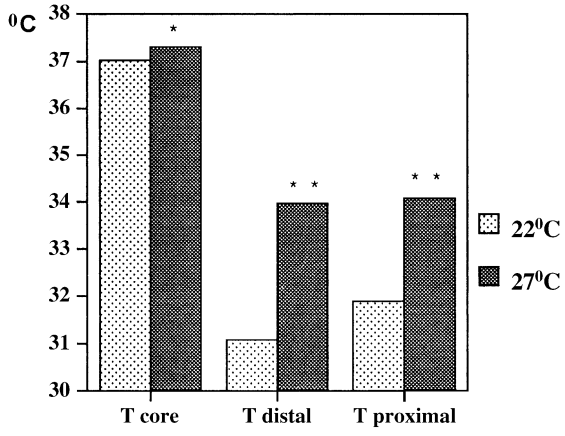

Fig. 1. Average body temperature measured during 2 subsequent days (16 h per day) at ambient temperatures of 22 and 27 °C in women ($n = 8$). T core = core temperature (rectal), T distal = distal skin temperature (average of T hand and T foot), T proximal = proximal skin temperature (average of T forehead, T thigh, and T collarbone). At 22 and 27 °C, respectively: T core 37.04 ± 0.3 and 37.39 ± 0.3 °C; T distal 31.13 ± 0.6 and 33.89 ± 0.3 °C; T proximal 32.02 ± 0.4 and 34.05 ± 0.35 °C. * $P < .05$; ** $P < .001$, for differences between ambient temperatures.

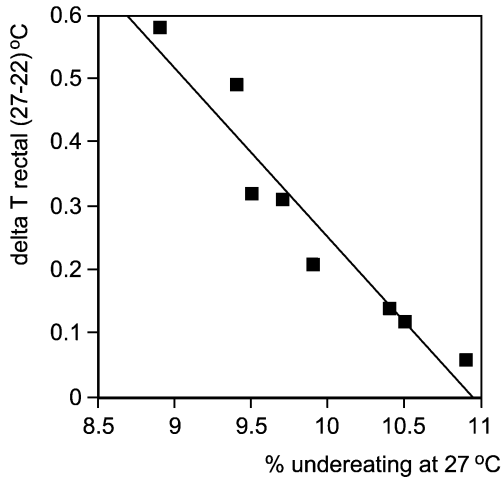

Fig. 2. Relationship between percentage undereating and increase in rectal temperature at 27 °C in normal-weight women; $n = 8$. $y = -3x + 3$; $r^2 = .9$; $P < .001$.

On the ad libitum feeding days at both ambient temperatures, the subjects were in a negative EB. At 22 °C EI was 90.3 ± 19% of EE, and at 27 °C EI was 90.7 ± 11.3% of EE ($P = .9$). The differences between EI and EE were statistically significantly different from 0 ($P < .01$), but these differences did not differ between the ambient temperatures ($P > .5$). At both ambient temperatures ad libitum EI was 90–91% of EE ($P > .9$). At 27 °C, percentage undereating was inversely related to the increase of rectal temperature $y = -3x + 3$; $r^2 = .9$; $P < .001$ (Fig. 2).

3.4. Energy expenditure

In EB, 24 h EE had decreased by 10 ± 2% at 27 °C, as compared to that at 22 °C (8.9 ± 1.3 MJ/day vs. 9.9 ± 1.5 MJ/day) ($P < .001$).

This consisted of a decrease in DIT ($P < .01$) and in AEE ($P < .01$), with an almost stable SMR (see Table 1 and Fig. 3). The standard deviation of the individual SMR measurements was between 0.005 and 0.01 MJ/day, indicating an error of 0.2 ± 0.01% of SMR. The accuracy of RMR (SMR + DIT) and of AEE is given by the 95% confidence interval of the individual regression lines of AEE vs. radar counts, which was 2 ± 0.1% of RMR. Adding the square variances, this results in an overall error of 2.6% of 24 h EE.

EE as a function of FFM was significantly lower at 27 °C, compared to that at 22 °C ($P < .01$), i.e., the intercept differed significantly, but the slopes did not differ ($r = .9$, for both equations).

Table 1
24 h EE, SMR, DIT, AEE, PAL, RQ, and FQ of eight lean women during EB with a standardized physical activity protocol and clothing at 27 °C (Day 2 of EB), compared to at 22 °C (Day 1)

	22 °C	27 °C
24 h EE (MJ/day)	9.9 ± 1.5	8.9 ± 1.3***
SMR (MJ/day)	5.6 ± 0.7	5.9 ± 0.7
DIT (MJ/day)	1.0 ± 0.2	0.7 ± 0.1**
DIT (% of EI)	10 ± 2	7.5 ± 1
AEE (MJ/day)	3.3 ± 1.0	2.3 ± 0.6**
PAL (24 h EE/SMR)	1.8 ± 0.1	1.5 ± 0.1
RQ (24 h)	0.85 ± 0.02	0.88 ± 0.02*
RQ (12 h day)	0.86 ± .01	0.89 ± 0.02
RQ (12 h night)	0.81 ± 0.03	0.84 ± 0.04*
FQ	0.88 ± 0.004	0.88 ± 0.01

* $P < .05$.
** $P < .01$.
*** $P < .001$.

In the ad libitum feeding situations, EE was not significantly different from EE during EB, i.e., 9.9 ± 1.2 MJ/day at 22 °C and 9.0 ± 1.1 MJ/day at 27 °C.

The relative DIT was 7.5 ± 0.9% at 27 °C, and 10 ± 2.1% at 22 °C ($P < .01$).

AEE expressed as a function of radar output showed a different slope at 27 °C, compared to that at 22 °C ($P < .05$), indicating a higher AEE efficiency at 27 °C, particularly at the relatively higher intensity activities. The radar output corrected for the offset point for the daily activities at both temperatures was on average 4461 counts/min at 22 °C, and 4267 counts/min at 27 °C ($P = .4$), confirming that the daily activities were comparable during both ambient temperatures. During the 30-min bouts of extensive aerobic activity, at both ambient temperatures, rectal temperature increased by 0.2 ± 0.2 °C ($P > .05$). The total increase in EE during this activity was on average 4.5 ± 1.5 kJ/min or 60% at both ambient temperatures.

Although the food consumed had the same FQ for both ambient temperature conditions, RQ was increased at 27 °C (Table 1). This increase appeared to be due to the increase in RQ during the night.

3.5. Energy intake

During the 24-h ad libitum feeding situations (Day 2 at 27 °C ad lib and Day 2 at 22 °C), EI was 8.9 ± 2.0 MJ/day (22 °C), and 8.2 ± 1.4 MJ/day (27 °C), respectively. Decreases in EI were correlated with decreases in EE ($r = .88$; $P < .001$). The reduction of EI (10 ± 3%) at 27 °C itself was not statistically significant ($P = .06$). ED of total consumption (food and drinks) was decreased at 27 °C by 15 ± 2%, compared to that at 22 °C ($P < .01$). ED was 3.4 ± 0.4 kJ/g at 22 °C and 2.9 ± 0.5 kJ/g at 27 °C, respectively. At both ambient temperatures, ED was related to EI (at 22 °C: $r = .83$; $P = .02$, at 27 °C: $r = .97$; $P = .0001$). Moreover, the change in ED was positively related to the change in EI ($r = .8$; $P < 0.01$). Thus, the tendency of a significant reduction in EI (10 ± 3%) was related to the statistically significant reduction in ED (15 ± 2%).

Meal frequency (number of eating occasions/day) remained constant, i.e., three meals and three snacks a day. Neither the macronutrient composition [carbohydrate/protein/fat: 57/13/30 percentage of energy (22 °C); 56/14/30 percentage of energy (27 °C)], nor total weight of consumption (food and drinks) [2.6 ± 0.7 kg (22 °C); 2.9 ± 0.5 kg (27 °C)] was statistically significantly different ($P > .05$).

At a closer inspection of the selection of food and drinks, it appeared that the decreased ED of food intake at 27 °C compared to at 22 °C was due to the following. Although all the food types that were offered were consumed, 40 ± 2% of total EI of the lower energy dense foods (0–7.5 kJ/g) were consumed instead of 37 ± 2% (at 22 °C) and 10 ± 1.5% of the higher energy dense foods (15–22.6 kJ/g) were consumed, instead of 13 ± 1.5% (at 22 °C). There was no significant difference in the intake of water as such, or of coffee or tea, between both ambient temperatures. The appetite profile did not show any statistically significant

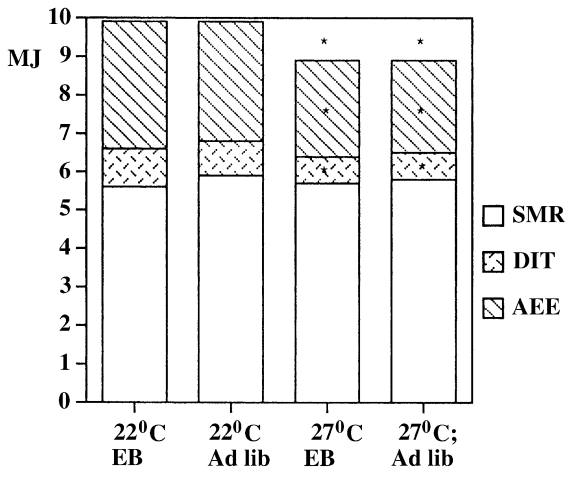

Fig. 3. EE at 22 and 27 °C in normal-weight women; $n = 8$; SMR: sleeping metabolic rate; DIT: diet-induced thermogenesis; AEE: activity-induced energy expenditure. * $P < .01$, compared to the similar day at 22 °C.

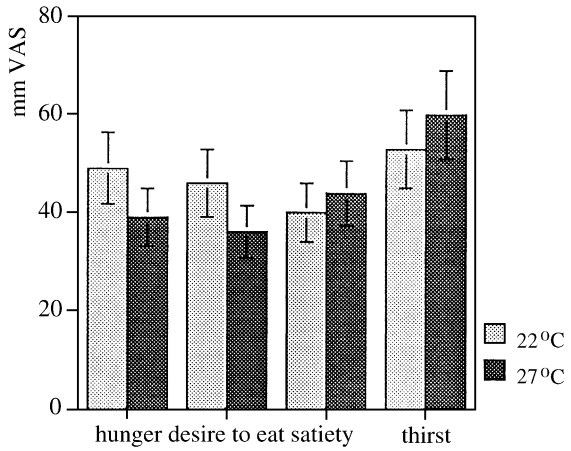

Fig. 4. Average VAS ratings of the appetite profile in normal-weight women at 22 and 27 °C being fed ad libitum, $n = 8$.

differences between the two days with different temperatures, neither while the subjects were fed in EB, nor when they were fed ad libitum (Fig. 4).

3.6. Comfort

Average comfort ratings on the VAS approximated 75, and irritation was low, with no statistically significant differences between the two situations with different ambient temperatures, either with being fed ad libitum, or in EB.

3.7. Relationship between body temperature or EE and EI

Multiple regression analyses on the contributions of changes in body temperatures (both rectal and skin temperatures) and EE to changes in EI and ED showed the following. The reduction in EI and ED at 27 °C, as compared to that at 22 °C, was primarily related to the increase in proximal and distal skin temperatures (t values: proximal temperature: 4.3; distal temperature: 4.0; both $P < .01$). Secondarily, the EI and ED reductions were related to the residuals of the regression of EE vs. FFM (t value: 3.2; $P < .01$).

4. Discussion

Short-term (48 h) exposure to an ambient temperature in the thermoneutral zone, i.e., 27 °C (81 °F) of normal-weight women who were acclimated to an ambient temperature of 22 °C (72 °F) caused a significant reduction in energy metabolism. This reduction consisted of a reduction in DIT and activity-induced thermogenesis, and a trend of a reduction in EI related to a significant reduction in ED of the food chosen. At the same time, related to this reduction in energy metabolism, rectal and skin body temperatures were increased. Reduction in EE was present when the subjects were fed in EB, while clothing and daily activities were standardized. A tendency to a reduction in EI paralleled the reduction in EE. Despite increases in rectal and skin temperatures at 27 °C, comfort ratings, which were not significantly different between both ambient temperatures, showed that the women felt comfortable at both temperatures. Since the reduced EE showed the same relation with FFM as the original EE did, only the level of EE was reduced at 27 °C. Although 24 h EE was reduced at 27 °C, SMR was not. The reduced EE in the thermoneutral zone is consistent with the findings reported previously [13–20]. The absence of a reduction of SMR seems to be different from some previous findings (i.e. Refs. [17,19]), reporting a significantly higher BMR at 22 °C, compared to that at 28 °C. This may be due to differences between BMR and SMR measurements. The BMR measurements lasted one [19] or two [17] hours, while the SMR measurements were executed during the three hours of subject-specific lowest EE, also indicated by lowest radar counts, usually between 3:00 and 6:00 a.m. Another reason for the difference in these results might be that in the previous studies subjects were nude, whereas our subjects slept under a duvet. This indicates that the increased BMR at 22 °C might be due to mild cold whereas finding no difference in SMR might be due to thermal comfort.

24 h DIT was reduced at 27 °C, compared to 24 h DIT at 22 °C. This concerned the absolute value, which was partly due to the lowered EI, but also the relative value, i.e., the percentage of total EI. At both ambient temperatures, the macronutrient composition of the food was the same, and FQ was the same, so this cannot have affected the DIT [38]. Since the difference in 24 h DIT cannot completely be explained by the difference in EI, at 27 °C it was especially the facultative component of DIT being decreased [24–26,38]. We defined this part of EE as NST3 [41], being the part of nonshivering thermogenesis that is included in RMR.

24 h AEE was reduced, at 27 °C, compared to that at 22 °C, despite the identical and standardized activities protocol under both circumstances. It might be expected that subjects would be less active at higher ambient temperatures, but here we prevented this reaction by the standardized extensive daily-activities program. The similar level of activity is confirmed by the similar radar output. It is possible that less energy has been spent on nonexercise activity thermogenesis (NEAT), and that at 27 °C activity might be slightly more efficient by a modification in the temperature sensitivity of enzyme activity. EE during moderate aerobic exercise increased moderately by an average of 4.5 ± 0.5 kJ/min, or 60%. Larger increases in physical activity are usually accompanied by increases in deep body temperature, closely related to the intensity of work relative to maximum work rate [42] and relatively independent of ambient temperature [43]. We observed a small, statistically nonsignificant increase in the rectal body temperature during the moderate aerobic exercise bouts, at both ambient temperatures, due to the moderate activities the subjects executed. The errors of the measurements of SMR, RMR, and AEE of $0.2 \pm 0.1\%$ and $2 \pm 0.1\%$ were smaller than the actual differences in EE of 5.4%, 30%, and 30%, respectively. Also, the overall error of 2.6% was smaller than the difference in total EE of 10%.

24 h RQ was significantly higher at 27 °C than at 22 °C, due to the 12 h RQ values during the night. This suggests a temperature or EE dependency of substrate oxidation, i.e., a higher carbohydrate oxidation at higher ambient temperatures, despite identical FQ values. Because EE is lower at 27 °C than at 22 °C, the glycogen reserves lasted longer at 27 °C, and therefore RQ did not drop as much as at 22 °C during the night. Thus, we conclude based upon the decreased energy requirements for DIT and AEE in the thermoneutral zone that in women in EB, while clothing or daily activities are excluded from temperature regulation, DIT and AEE contribute significantly to temperature regulation. There was a tendency for reduction in EI at 27 °C, which was related to the decrease in EE, without a change in the appetite profile or comfort. In the ad libitum feeding

situation at both ambient temperatures, EI was 90.3–90.7% of EE (P=.9). It should be noted though that during the 24-h periods at both ambient temperatures of ad libitum feeding, the subjects were in a negative EB through a decreased EI. However, the energy deficiency was similar, so EI still can be compared between the two ad libitum feeding periods during the different ambient temperatures. The change in EI appeared not to be statistically significant in itself (P=.06), due to the high variability of food intake in the ad libitum feeding situation and to the relatively small number of subjects. The relationship between the decrease in EI and EE was statistically significant, and the change in ED was statistically significant, while ED was related to EI [44].

Both the EI and ED changes were primarily related to the changes in proximal and distal skin temperatures, and secondarily to the change in EE, as was revealed by multiple regression analysis. Moreover, the inverse relation between undereating and increase in rectal temperature showed individual variation in body temperature regulation, in that the less one ate, the less rectal temperature increased. This suggests that food intake regulation by the body is a mechanism of thermoregulation and vice versa. In homeothermic animals, feeding activity might be one of the activities that might be stopped by a thermoregulatory response to prevent hyperthermia in a relatively warm environment [48–51].

The present study shows a similar reduction in EI with increasing temperature (140 kJ/°C) as a result from a previous long-term study [29]. From a field study in which the 50–200 men examined were fully acclimated to the particular environment in which they were living, although clothing and activity were not standardized, a decrease of 125 kJ/°C was reported [29]. Both this figure and ours are higher than the 60 kJ/°C reported in a 1950 FAO report [45]. Thus, the reduced EE at the higher ambient temperature, while executing the same activity protocol and wearing the same clothing, indicates that EI needs to be adapted to prevent a positive EB. This was shown spontaneously in this study, through the decreased ED. It might be expected that thirst ratings would have changed to indicate the decrease in ED of food consumption. During the first rating at 27 °C, before breakfast, thirst was not significantly increased (P=.10), and in the course of the day the nonsignificant difference compared to that at 22 °C diminished; obviously, the type of consumption was adjusted to the level of thirst.

Food intake at 27 °C with a reduced ED was not indicated by the appetite profile. Levels of hunger and satiety had not changed at 27 °C, despite ingesting about 10% less energy than at 22 °C, and despite being in a slightly negative EB. This suggests that the appetite profile was the result and not the cause of food intake. Also, comfort did not affect food intake since these ratings did not differ between the two ambient temperatures. One other study demonstrated that changes in ambient temperature did not modulate feelings of hunger significantly [46]. Some field studies show similar results, i.e., an inverse relationship between ambient temperature and food intake during chronic exposure of troops to different climate conditions [28,29], or no correlation between food intake of several groups of military personnel and climate [27]. These studies are based upon self-reported intake of military personnel, and might therefore partly be susceptible to potential errors of underreporting [47].

In conclusion, we have shown that women, in EB, during short-term exposure to the thermoneutral zone, being prevented by adapting clothing or activities, showed an adaptation in EE by decreasing DIT and AEE. The increased RQ at 27 °C indicated a glycogen sparing effect. A relationship between food intake regulation and thermoregulation is suggested by:

the decrease in EI at 27 °C (by decreasing ED of foods) during ad lib feeding being primarily related to the increase in skin temperature (proximal and distal);
relative undereating at 27 °C being inversely related to the increase in rectal body temperature.

The question remains whether this short-term adaptation to the thermoneutral zone sustains on the longer term.

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